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GAMETOGENESIS AND REPRODUCTIVE PERIODICITY OF THE SUBTIDAL SEA ANEMONE *URTICINA LOFOTENSIS* (COELENTERATA: ACTINIARIA) IN CALIFORNIA

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ABSTRACT

Sexual reproduction of the actiniid sea anemone *Urticina (= Tealia) lofotensis* was studied for one year (1976–1977) in 105 specimens collected by hand monthly at 7–16 m in Carmel Bay, California. Gametogenesis, evaluated by light microscopy, is typical for an actinian. Oocyte maturation is asynchronous, even within a mesentery, whereas spermiogenesis of each male is synchronous. Each oocyte is associated with a trophonema, and eggs may exceed 1200 μm in diameter. The study population is dioecious, with a significant excess of females. Gonad indices and histological data indicate that the period of maximum female ripeness ends in December as the male maximum begins. The spawning peak appears to occur then, just as water temperature begins to fall from its annual high. Some females contain large oocytes and seem to release eggs throughout the year. Greatest reproductive quiescence is in April and May, when water temperature is at its minimum.

INTRODUCTION

Most studies of sea anemone reproduction have dealt with specimens collected intertidally; subtidal studies have relied on dredged material. Although reproductive studies on other subtidal coelenterates have been done with the aid of diving (*e.g.*, Ostarello, 1973; Rinkevich and Loya, 1979), ours is the first published study of subtidal sea anemone reproduction based on hand-collected specimens. It therefore adds a new dimension to the growing body of research on sexual reproduction of Pacific North American actinians begun two decades ago (*e.g.*, Ford, 1964; Spaulding, 1971; Siebert, 1974; Dunn, 1975; Siebert and Spaulding, 1976; Jennison, 1978, 1979; Sebens, 1981).

Urticina lofotensis (Danielssen, 1890) is a vivid crimson actiniid sea anemone with white verrucae 1–3 mm in diameter that make it appear polka-dotted or, in contraction, vertically striped (Fig. 1). Along the U. S. Pacific coast, its habitat is almost exclusively rocky subtidal. Only rare animals are exposed by minus tides, which probably accounts for the lack of biological information about the species. One of five named members of *Urticina* in the northeastern Pacific (the others are *U. columbiana, U. coriacea, U. crassicornis,* and *U. piscivora*), *U. lofotensis* ranges from Alaska to the Channel Islands (Hand, 1955; Sebens and Laakso, 1978).

In using the name *Tealia lofotensis* for this organism, Hand (1955) identified it with that which Danielssen (1890) described from Norway as *Madoniactis lofo-*

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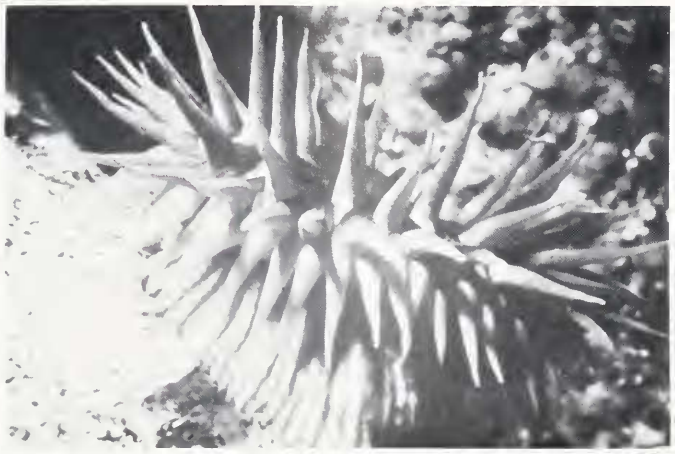

FIGURE 1. Typical posture of *Urticina lofotensis* on rock substratum. Specimen is approximately 100 mm across.

tensis. The name *Urticina* has priority over *Tealia,* which is, in turn, senior to *Madoniactis* (Williams *in* Manual, 1981). Manual (1981), following Stephenson (1935), synonymized the European *T. lofotensis* with *Bolocera eques* Gosse, 1860, which has been known as *T. crassicornis,* calling it *U. eques.* Manual (1981) questionably included Hand's *T. lofotensis* in the synonymy as well. It seems prudent to maintain current usage of *Urticina* species names for animals of the north Pacific pending further systematic study since anemones called *U. lofotensis* and *U. crassicornis* are easily separable on the Pacific coast of North America (Hand, 1955; Sebens and Laakso, 1978), and both seem to differ from the European *U. eques* as *per* Stephenson (1935) and Manual (1981).

Stephenson (1935) and Manual (1981) summarized literature on, and morphology of, European animals called *Urticina lofotensis.* Hand (1955) and Sebens and Laakso (1978) described the anatomy of northeast Pacific anemones of the same name. Data on reproduction are confined to remarks on size of gametes and distribution of gonads.

MATERIALS AND METHODS

Between 4 and 12 anemones were collected at four-week intervals from 9 November 1976, to 12 October 1977, by SCUBA diving from a boat off the rocky north end of Carmel River State Beach, California (36°32′25″N, 121°55′53″W). The bottom is characterized by rocky rubble interspersed with small sandy areas and granitic boulders, most 3–5 m in diameter, some 7 m tall and rising to within 3 m of the surface. Passages between boulders are subject to surge and scour, especially in winter, due to ocean swells coming directly from deep water offshore. The study area, approximately 200 by 100 m (Fig. 2), ranged in depth from 7 to 16 m. Anemones are scarce in water deeper than 16 m, and strong wave action and surge made collecting in water shallower than 7 m difficult or impossible during most of the year. An extension of the Carmel submarine canyon near the study area influences wave action, upwelling, and temperature fluctuation.

A different portion of the study area was sampled each month by two divers swimming along a selected compass heading, arbitrarily removing anemones from

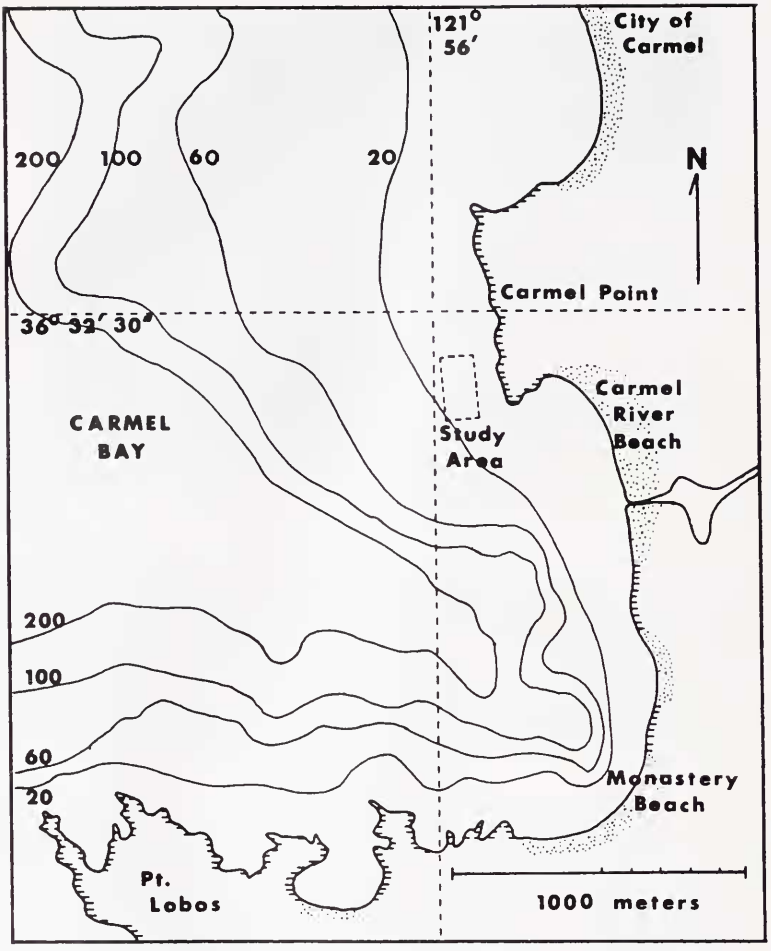

FIGURE 2. Map of southern Carmel Bay, California, indicating location of the study area. Depth contours in meters.

the substratum. Measuring pedal disc diameter prior to collecting was attempted but proved difficult in the surge, so was discontinued. Animals were carefully scraped and peeled from the rocks using a dull knife blade. To prevent contact among animals and to keep track of oocytes released after collection, each animal was placed in a separate perforated plastic jar covered by a plastic screw cap. The containers, of minimal buoyancy, could easily be transported by the diver in a nylon mesh bag. They were returned to the laboratory in a styrofoam cooler filled with sea water. Water samples from the cooler were examined microscopically after removing the jars. No eggs were found, but much undigested food expelled by the anemones during transit was always evident.

In the laboratory, the animals (in jars) were placed in running sea water. The next morning, after they had expanded fully in liter beakers of sea water, half the fluid was replaced by 100–200 ml of 10% $MgCl_2$ in sea water. Complete relaxation, until a pinch on several of the by-then flaccid tentacles elicited no response and the

oral disc was expanded and darkened, required several hours. If narcotization was slow, additional relaxant was added; this was most often necessary with specimens over 70 mm basal diameter.

Anemones were fixed in Bouin's solution (Humason, 1962) made with undiluted sea water. Despite seemingly thorough relaxation, many contracted somewhat when fixative was added. About 10% contracted violently, everting the actinopharynx, which made dissection difficult. At least a week in Bouin's was allowed for complete fixation.

Prior to dissection, pedal disc diameter was measured. The anemones were bisected across the column, 10–20 mm distal to the base. Food objects and gonadal tissue were removed with forceps under a dissecting microscope. Gonads were preserved in Bouin's solution. Mesenteries were counted in the basal section.

Each animal, minus its gonads, was dried for six days in a vacuum desiccator at 60°C, and weighed immediately upon removal. Dry weight of gonad not set aside for histological examination was determined after desiccation for 24 h. Four large blotted pieces of gonad from each anemone were weighed prior to dehydration, cleared, and embedded in paraffin. Their approximate dry weight added to that of the desiccated pieces yielded the total dry gonad weight. The relation of dried gonad weight to that of the entire animal, encompassing gonad as well as body, constituted the gonad index (GI).

Seven μm serial sections of gonad were stained with Harris' hematoxylin and eosin (Humason, 1962). Fifty oocytes from each anemone were measured in sections that included the nucleolus, which reduced the possibility of measuring the same cell more than once. The two longest perpendicular diameters were averaged in irregularly shaped oocytes. Eggs smaller than 25 μm were difficult to measure accurately, so were not included in the count.

Maturity of male gonads was scored as follows: stage 1—gonadal packets containing only spermatogonia; stage 2—packets with spermatogonia, spermatocytes, and the first noticeable tailed sperm; stage 3—fully mature packets containing predominantly sperm. Animals with follicles at a maturity level between stages 1 and 2 were placed subjectively in one or the other; those with packets between stages 2 and 3 were classified according to the relative abundance of sperm. For example, a male with packets half full of mature sperm was at stage 2½.

Surface water temperatures were obtained from the California Department of Fish and Game's Marine Culture Laboratory at Granite Canyon, south of the study area. Water temperatures taken at depth on several collecting dives during the year generally agreed with the data from Granite Canyon.

Results

Sexuality and morphology

Urticina lofotensis is dioecious: 54 females, 34 males, 17 animals lacking gonads, and no hermaphrodites were collected. Sex determination was not possible externally. Even under low magnification, immature gonads of both sexes appeared similar, but at later developmental stages were distinguishable by color and form.

Male gonads were bright red, the color dulling considerably after fixation. The greatly elongated, pleated gametogenic portion along the inner mesentery edge (Fig. 3a) was easily located and removed during dissection.

Female gonadal tissue was less convoluted, the oocytes were contained within indistinct clusters along the mesentery edge. Mature clusters resembled bunches of grapes. In Bouin's fluid this tissue was generally yellow or brown, and loose eggs

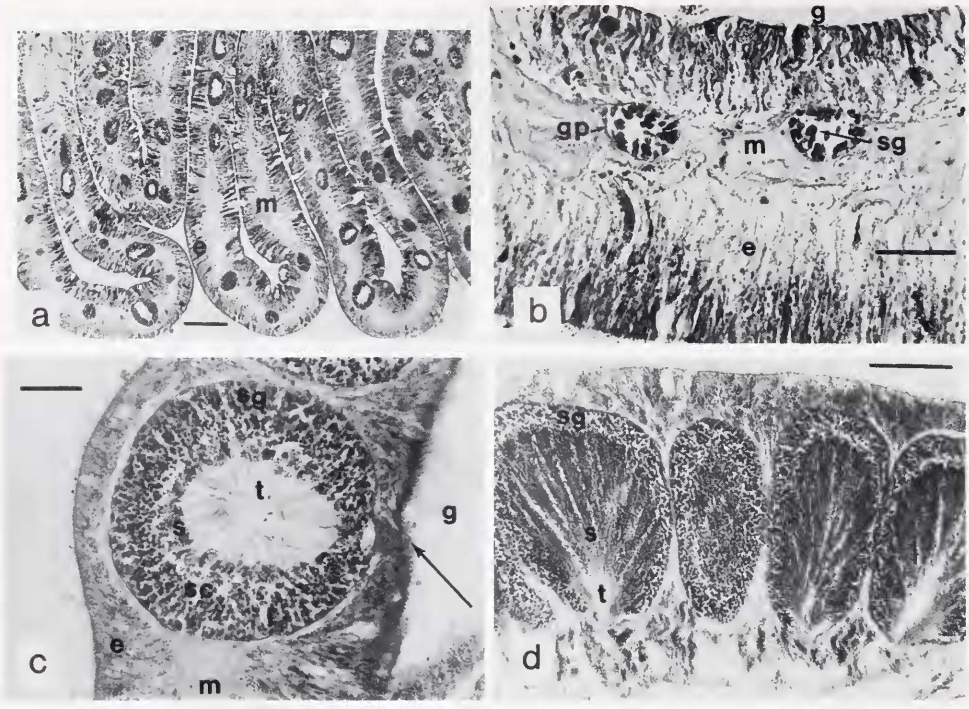

FIGURE 3. a) Section through gametogenic portion of one mesentery from male anemone. Scale bar = 100 μm. b) Section through early gonadal packets with spermatogonia (stage 1). Scale bar = 30 μm. c) Section of stage 2 gonadal packet with numerous tailed gametes. Note layering. Arrow indicates plug-like structure. Scale bar = 30 μm. d) Mature gonadal packets (stage 2½) with abundant immature gametes. Scale bar = 50 μm. e = endoderm; g = gastrovascular cavity; gp = gonadal packet; m = mesoglea; s = spermatozoa; sc = spermatocytes; sg = spermatogonia; t = sperm tail.

were yellow. Sometimes oocytes/ova were expelled during fixation and several females were collected with eggs among the tentacles and adhering to the oral disc; diameter of these gametes was 700–800 μm. Spawning was never observed, and no larvae were found in or on any anemone.

The number of mesenteries in *Urticina lofotensis* corresponds to the number of tentacles and is the same distally and proximally. In 26 anemones of all sizes, it ranged from 47 to 77 pairs, and did not correlate strictly with animal size as determined by pedal disc diameter or dry weight. Generally, however, larger animals had more mesenteries. Many weighing from 12 to 15 g had just over 50 pairs, although a female with 77 pairs weighed only 8 g.

Oogenesis

The most immature germ cells observed were in the endoderm, ranged from 10 to 30 μm, and contained a nucleus about half their diameter (Fig. 4a). Large concentrations of cells occurred near the junctions of germinal and non-germinal mesentery tissue, but some were scattered in the endoderm, many near mature oocytes (Fig. 4b).

The smallest oocytes in the mesoglea were 20–50 μm in diameter. Previtellogenic cells stained a characteristic deep blue with hematoxylin and eosin; yolk platelets

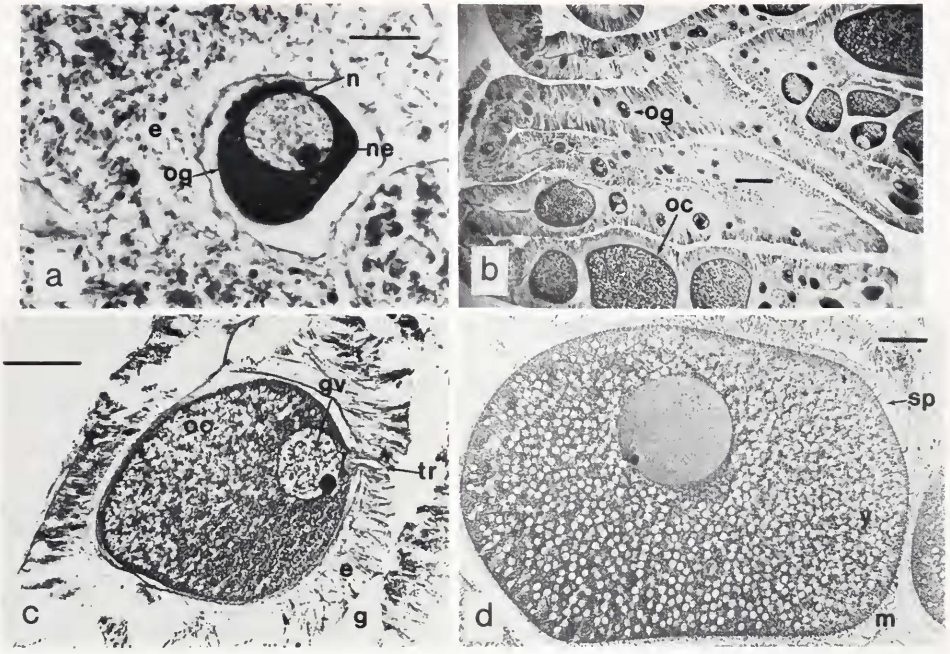

FIGURE 4. a) Section of early female gamete in the mesenterial endoderm. Scale bar = 20 μm. b) Section through a female gametogenic mesentery containing gametes in many stages of development. Scale bar = 100 μm. c) Section of an oocyte with a trophonema. Scale bar = 50 μm. d) Section through a large, yolky oocyte with spines. Scale bar = 50 μm. e = endoderm; g = gastrovascular cavity; m = mesoglea; n = nucleus, ne = nucleolus; oc = oocyte; og = immature germ cell; sp = spines; tr = trophonema; y = yolk granules.

took up eosin predominantly, giving larger cells a distinct pink color. During vitellogenesis, the oocyte nucleus (germinal vesicle) moved peripherally to either side of the cell, adjacent to the mesenterial endoderm, and did not increase appreciably in size. Nuclei of larger cells therefore appeared relatively small. Oocytes of all sizes contained one darkly stained, round nucleolus 10–20 μm in diameter.

In oocytes undergoing vitellogenesis and some previtellogenic cells, a tubular trophonema connected the cell through the mesoglea and endoderm to the gastrovascular cavity (Fig. 4c), its end flaring where it joined the oocyte. Attachment to the gamete was always in proximity to the germinal vesicle. Trophonemata were less prevalent in larger oocytes, but their remnants—small pieces of tissue adjacent to the nucleus—were common. Spines 5–15 μm long covered the surface of most larger oocytes. They were especially apparent where the mesoglea had pulled away from the oocyte during fixation (Fig. 4d). Each oocyte within the mesentery had a germinal vesicle.

Spermiogenesis

All mesenteries of an individual contained sperm follicles of uniform maturity. Spermatogonia were not identifiable in the endoderm. The smallest sperm packets in the mesoglea were round to ovoid 20–50 μm across, and contained up to 30 spermatogonia, each approximately 3–5 μm in diameter, with an indistinct nucleus half or less the diameter of the cell (Fig. 3b).

Spermatogonia lined the periphery of the growing follicle while smaller spermatocytes (2–3 μm) occurred centrally, layering becoming pronounced with increasing numbers of cells. At a later stage, spermatids (1 μm diameter), in clumps of four to eight cells, occupied the packet's center. By this stage the follicle was 33–50% the width of the mesentery. Shortly thereafter the lumen of the packet opened slightly, and tailed sperm with heads approximately 1 μm in diameter became evident (Fig. 3c).

Mature follicles expanded to nearly the full width of the mesentery (Fig. 3d). They were lined with developing gametes, spermatogonia and spermatocytes at the periphery, spermatids more centrally, and spermatozoa bundled with their tails together in the lumen. A few mature follicles occurred in spawned-out males, suggesting that all sperm are not always shed. Some spawned-out males also had immature spermatogonial packets.

Gonad Cycles

Figure 5 indicates the relative size frequencies of oocytes measured in section from the 54 female anemones collected. Although smaller oocytes were disproportionately represented due to their relatively large nuclei, changes in average gamete size through the year were evident. Cells between 50 and 150 μm predominated in all animals, and very large oocytes (450–600 μm) were also present all year, although in much smaller and varying quantities. Small oocytes made up a large percentage of gametes during winter (November to February), and on into spring, but represented a much smaller proportion during later spring and summer. Oocytes in the size classes of greatest frequency during winter averaged just under 100 μm. During summer (June through September), smaller oocytes decreased in frequency but had begun to increase again by October. Small quantities of large oocytes (350–500 μm) were present in November and especially December. By January, most had disappeared.

Proportions of large (pink-staining) oocytes in the 50 measured gametes are displayed in Figure 6, which confirms their relatively high frequencies in some anemones during November and December, and their generally low prevalence in January and April. The increase from May through September is more evident in Figure 6 than in Figure 5. Animals collected during September contained the greatest

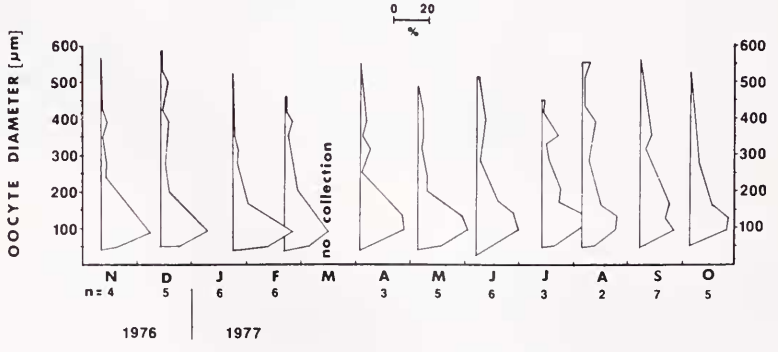

FIGURE 5. Size-frequency polygons for diameters of 50 oocytes from each female specimen of *Urticina lofotensis*. Each polygon indicates cumulative size frequencies for that month. One of the six females collected in December and one of the seven collected in January contained only loose oocytes.

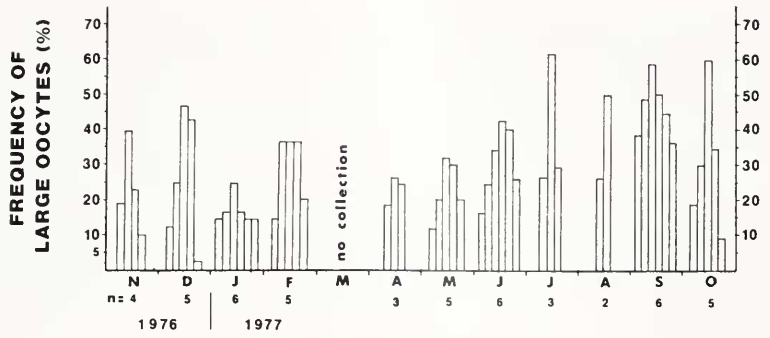

FIGURE 6. Histograms showing the proportion of large oocytes among the 50 cells measured from each female specimen of *Urticina lofotensis*. Each histogram represents an animal. One of the females collected in February and one collected in September contained only small oocytes.

proportion of large oocytes. Percentage of large cells in most females had dropped considerably by October.

Maximum female GI was 16.4% in a 10.0 g animal collected in November. The largest female, from the June collection, had a weight of 17.3 g and a GI of 15.1%; the smallest female, taken in October, weighed 4.4 g and had a GI of 3.4%. Average female GI gradually declined from November to its nadir in May, generally paralleling the pattern in males and surface water temperature (Fig. 7). Although it had just begun to increase (Fig. 6), large oocyte frequency was also low in May, when oocytes less than 200 μm in average diameter were predominant (Fig. 5).

The gonad cycle of males is shown in Figures 7 and 8. In April, when the largest male, weighing 19.3 g (GI 3.7%), was collected, and in May, when the smallest, weighing 4.1 g (GI 0.7%) was collected, gonad indices were low and males contained only spermatogonia. The first sperm had developed by June when, as with females, GI abruptly increased. From an August low (based on one male with 47 pairs of mesenteries, several residual sperm packets in its immature gonads, and a GI of 1.6%) almost equal to that of May, male GI increased through October, with a

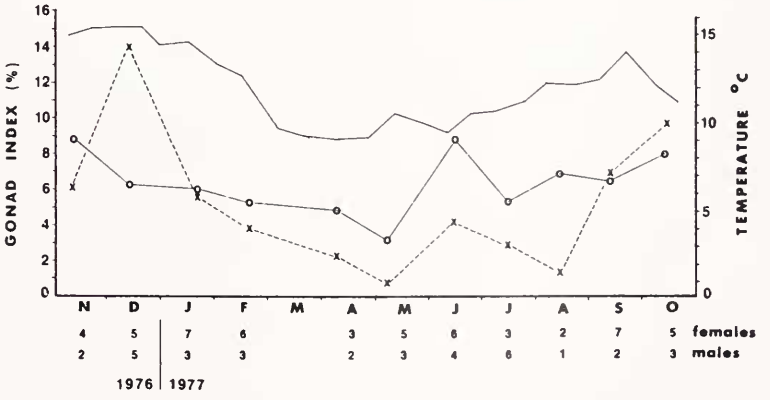

FIGURE 7. Monthly average gonad indices of female (--- O ---) and male (--- × ---) specimens of *Urticina lofotensis*, with number of specimens indicated below. Surface water temperatures (-----) are biweekly averages. No collection was made in March.

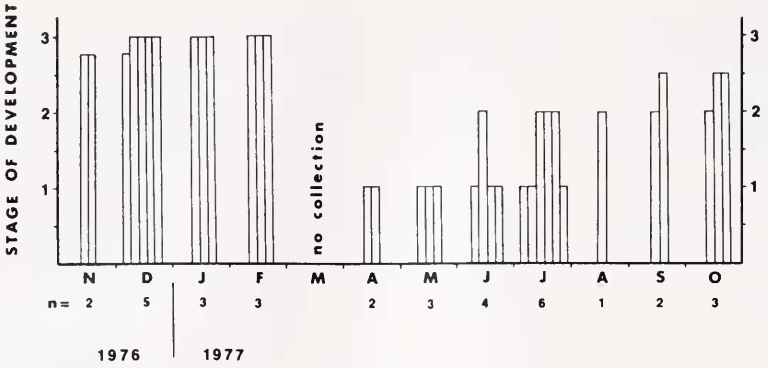

FIGURE 8. Histograms showing maturity of male specimens of *Urticina lofotensis* through the year. Each histogram represents an animal. See text for explanation.

concomitant sperm buildup. In September and October, gonadal packets were half full of sperm. Males collected in winter had follicles filled with sperm. The highest average monthly GI was in December (14.1%) when the five sea anemones had predominantly stage 3 gonadal packets. Among them was the second largest male collected (18.7 g), which had the highest individual GI, 22.7%. Although mature follicles predominated through February, average male GI decreased from December through May. GI generally increased with anemone size for both sexes (Table I).

Anemones with no gonads visible during dissection were not sectioned. All but two of these animals had dry weights less than 7.6 g (Table I), indicating that they were probably juveniles. The other two, both collected in February, were 8.0 and 13.5 g.

Natural history notes

Approximately 20% of dissected anemones contained shells, both empty and with animals, of the small (10–20 mm) gastropod *Calliostoma foliatum.* Most con-

TABLE I

Sex and gonad indices (+/− standard deviations) of Urticina lofotensis *by weight class*

Anemone dry weight (g)	Number of individuals			Average gonad index	
	Female	Male	Sterile	Female	Male
<3.9	0	0	2	—	—
4–5.9	4	3	5	3.6+/−3.0	1.4+/−1.0
6–7.9	5	6	8	4.4+/−2.1	3.5+/−3.0
8–9.9	14	5	1	5.5+/−4.4	6.9+/−5.3
10–11.9	13	13	0	7.7+/−4.9	5.7+/−5.1
12–13.9	9	3	1	5.5+/−3.2	7.3+/−2.8
14–15.9	6	2	0	9.7+/−2.5	8.8+/−1.2
16–17.9	3	0	0	11.4+/−3.4	—
18–19.9	0	2	0	—	13.2+/−13.4
	54	34	17		

Anemone dry weight includes body and gonad.

tained one shell, but a few had up to four. Other ingested objects included unidentified gastropod shells, crustacean body parts, bryozoans, pieces of algae, one 15 mm specimen of *Corynactis californica,* a 30 mm feather, a ctenophore 80 mm long, a 35 mm bat star (*Patiria miniata*), and a 100 × 50 mm flat abalone shell (*Haliotis wallalensis*) that was lodged across the actinopharynx of an anemone with basal diameter 60 mm.

Despite thorough searches of algal holdfasts, cracks, and caves with a diving light during many dives in the study area and elsewhere in Carmel Bay, no anemones less than 30 mm basal diameter were found. It is possible that very small animals were overlooked because of low numbers, being covered with debris (large animals often have material attached to their verrucae), or being hidden under algae.

Discussion

Sexuality and morphology

Distribution of gametogenic mesenteries in *Urticina lofotensis* is characteristic of the genus, the first ten pairs, including the directives, being sterile (Hand, 1955). All other mesenteries may be, but are not necessarily, gametogenic. The maximum of 77 pairs correlates well with Hand's (1955) data, but Sebens and Laakso (1978) reported considerably more. The regular arrangement of mesenteries implies that asexual reproduction does not occur in this species. [J. Brumbaugh (pers. comm., 1982) observed an anemone of this species divide longitudinally in an aquarium at Sonoma State University.]

Space for gonads should increase in larger anemones, and more mesenteries should enhance fecundity. However, there was little correlation between amount of gonadal tissue and number of fertile mesenteries in an animal. In fact, large actinians with moderate numbers of mesenteries produced the greatest quantity of gonad. Several anemones lacking visible gonads had more mesenteries than some very fertile ones (a sterile 3 g individual had 54 pairs, as many or more than many fertile animals weighing up to 9 g). Anemones add mesenteries as they grow, typically to a species-specific maximum. They grow only if fed, though, and may shrink if starved (Chia and Spaulding, 1972), so size, mesentery number, and age are not necessarily interrelated. Sebens (1981) found gonad as a percentage of body volume to increase with gonad number which, in turn, increases with body size in *Anthopleura xanthogrammica* and *A. elegantissima,* the rise being more rapid in smaller than larger anemones. GI of the sea urchin *Strongylocentrotus purpuratus* increases with test diameter in small animals but not in large ones, despite internal space expanding isometrically with size. Metabolic factors seem to be responsible for this (Gonor, 1972).

Laboratory raised *Urticina crassicornis* 40 mm in diameter are 18 months old (Chia and Spaulding, 1972). Assuming a roughly comparable growth rate for *U. lofotensis* in the field, the smallest anemones observed during this study are at least a year old, and the smallest fertile ones at least a year and a half old.

Associated with an oocyte undergoing vitellogenesis is a trophonema. Recent experimental evidence (Larkman and Carter, 1982) substantiated speculation (Nyholm, 1943; Loseva, 1971; Dunn, 1975) that this tube functions in nutrient transfer from the gastrovascular cavity to the developing egg. It may also act as a channel for egg release (Carter, pers. comm.). Trophonemata have been found, although not always identified as such, in a cerianthid and many sea anemones belonging to several families, but seem to be absent in other actinians (*e.g.,* Nyholm, 1943; Loseva,

1971; Dunn, 1975, 1982; Riemann-Zürneck, 1976; Jennison, 1979, 1981; Larkman and Carter, 1982).

At the mesentery edge, some sperm packets have a plug-like structure (Fig. 3c) that may be homologous with a trophonema. On the other hand, the convoluted gametogenic mesentery of males has a large surface area that may facilitate nutrient transfer from the gastrovascular cavity through the thin layers of endoderm and mesoglea surrounding the gametes. Gamete release is probably facilitated for both sexes by proximity to the mesentery edge.

Sex ratio of *Urticina lofotensis* is significantly different from 1:1 (chi square = 4.54; $0.025 < P < 0.05$). Although it is remotely possible that sampling error is responsible, or that most of the 17 sterile individuals were male, the preponderance of females is probably real. Such an excess is known in a variety of temperate and tropical actinians (Dunn, 1982).

Oogenesis

Oogonia originate in the endoderm of anthozoan mesenteries. Dunn (1975) and Jennison (1979) reported that after migrating into the mesentery's central mesogleal layer, secondary oogonia cease mitosis and become oocytes. However, Loseva (1971) failed to locate oogonia in *Urticina crassicornis,* and the smallest female germ cells that Larkman (1981) identified in *Actinia fragacea* endoderm were oocytes.

Eggs of *U. lofotensis* grow to 700–800 μm (preserved diameter) before being spawned. Dunn (1975) estimated that ova from *Epiactis prolifera* fixed in Bouin's solution were approximately 65% of their actual diameter. Thus, oocytes of *U. lofotensis* may actually exceed 1200 μm in diameter. Ova in other actinians range from 70 μm (*Gonactinia prolifera;* Gemmill, 1921) and 110 μm (*Bunodosoma cavernata;* Clark and Dewel, 1974), to 750–800 μm (*Stomphia didemon;* Siebert, 1973) and 1100 μm (*Bolocera tuediae;* Gemmill, 1921). Eggs of *U. coriacea* are reportedly 600 μm in diameter (Gemmill, 1921) and those of *U. crassicornis* up to 700 μm (Gemmill, 1921; Chia and Spaulding, 1972).

Germinal vesicles of *Urticina crassicornis, Epiactis prolifera,* and *Anthopleura elegantissima* are aligned on either side of the cell, as in *U. lofotensis* (Loseva, 1971; Dunn, 1975; Jennison, 1979). In *Actinia equina,* by contrast, those of all oocytes within each mesentery are arrayed on the same side (Chia and Rostron, 1970). The trophonema abuts an egg adjacent to its nucleus, suggesting that one may influence the position of the other. Germinal vesicles of *Peachia quinquecapitata,* which seems to lack trophonemata, are randomly oriented (Spaulding, 1974). Staining of cytoplasm in a large primary oocyte indicated protein synthesis and high concentrations of RNA around the germinal vesicle (Dybas, 1973). Presumably the subunits for these compounds reach the egg through the trophonema, as do other precursors (Larkman and Carter, 1982). Large oocytes contain evenly distributed eosinophilic yolk granules. The same is true of *U. crassicornis* (see Loseva, 1971).

In *Actinia equina,* oogenesis is synchronous within, but out of phase between mesenteries (Chia and Rostron, 1970), whereas *Urticina crassicornis, Peachia quinquecapitata,* and *Anthopleura elegantissima* resemble *U. lofotensis* in being asynchronous within mesenteries (Loseva, 1971; Spaulding, 1974; Jennison, 1979). As in *U. lofotensis,* male gametes of *Actinostola crassicornis* ripen synchronously within but not between individuals (Riemann-Zürneck, 1978). Gametes of both sexes in all developmental stages occur in the same mesentery of hermaphroditic individuals of *Epiactis prolifera* (see Dunn, 1975). Heterogeneity of gamete size is known in such other marine invertebrates as hydrozoans (Kessel, 1968) and echinoids (Holland, 1967; Gonor, 1973b). Spawned gonads of *A. elegantissima* contain residual oogonia and previtellogenic oocytes that Jennison (1979) suggested either are pre-

vented from maturing or comprise the first gametes of the next reproductive period. Such hypotheses probably apply as well to *U. lofotensis.*

Spines reportedly range from 10 to 25 μm long in other actinians (Chia and Spaulding, 1972; Spaulding, 1972, 1974; Siebert, 1973, 1974; Siebert and Spaulding, 1976; Jennison, 1979). Dunn (1975) suggested that surficial structures 1.5–4 μm long on oocytes of *Epiactis prolifera* may be fixation artifacts. Loseva (1971) thought that spines on *Urticina crassicornis* oocytes might function in nutrient absorption from the mesoglea, while Siebert (1973) proposed that spines prevent polyspermy.

Oocytes are apparently released with the intact germinal vesicle containing a single nucleolus, so final maturation divisions must occur during or after spawning, perhaps even after fertilization, which must be external. Eggs of *Urticina crassicornis* mature before being spawned (Chia and Spaulding, 1972).

Spermiogenesis

Development of spermatogonia, which also arise in mesenterial endoderm, is like that in other anthozoans (Chia and Rostron, 1970; Chia and Crawford, 1973; Clark and Dewel, 1974; Dunn, 1975; Jennison, 1979). Discrimination of later spermiogenic stages is facilitated by layering of the gametes. Spermatids and the first spermatozoa can hardly be identified individually. In an ultrastructural study of the sea anemone *Bunodosoma cavernata,* Dewel and Clark (1972) reported that spermatocytes already possess a flagellum, making it difficult to distinguish between the latter stages of spermiogenesis, a problem Jennison (1979) also had in a light microscopic study of *Anthopleura elegantissima.* The germinal portion of the mesentery is resorbed after spawning of *A. elegantissima,* destroying the primary germ cells that had occupied the mature follicle's periphery (Jennison, 1979). The same may happen in *Urticina lofotensis.*

The 1 μm sperm heads of fixed *Urticina lofotensis* are similar in size to those of many other actinians (*e.g.,* Chia and Rostron, 1970; Dunn, 1975; Jennison, 1979, 1981), but smaller than some (Frank and Bleakney, 1976). Live spermatozoa of *U. crassicornis* have heads 1.5 × 2.0 μm (Chia and Spaulding, 1972), while those of *Peachia quinquecapitata* are 5.5 × 6.5 μm (Spaulding, 1972) and those of two species of *Anthopleura* are about 2 × 2–3 μm (Siebert, 1974).

Gonad Cycles

Gonad indices have been used to assess reproductive cycles of many marine invertebrates (*e.g.,* Pearse, 1970, 1978; Gonor, 1972, 1973a, b; Rutherford, 1973), but seldom sea anemones [Ford (1964) is an exception, and Sebens (1981) used a modified volumetric index]. Actinian gonadal tissue, not being concentrated in discrete organs, is not easily quantified. In addition, wet body weight is difficult to assess, which is why dry weights were used in this study. Histological observations acted as a check on GI (Giese and Pearse, 1974).

Data for *Urticina lofotensis* during 1976–1977 (Figs. 5–8) suggest an annual reproductive cycle with prolonged gamete release. Male and female gonad indices reached minimum values in May, when gametes of both sexes were immature and water temperature was at its minimum. Male GI attained its maximum in December; males were ripest December–February. Female GI had a high value in June and a slightly lower one in November; the highest proportion of ripe eggs was July–October.

Mesenteries of spawned-out female *Anthopleura elegantissima* were extensively ruptured (Jennison, 1979). This was never apparent in *Urticina lofotensis.* Large eggs of *A. elegantissima* disappeared after spawning, and several months later a new

cohort began to grow (Ford, 1964). Most female *U. lofotensis* studied contained histologically normal oocytes 600 μm or more in diameter throughout the year. These data explain the lower amplitude of female than male GI, and suggest that *U. lofotensis* may release ova intermittently rather than massively. This is supported by loose eggs in the enterons of many females. For example, such cells occurred in three of five females collected during October; four of them contained proportionately fewer large oocytes than any female taken the previous month. In contrast to prior months, no loose eggs were found in females during May, when large oocyte quantity was at a minimum.

The drop in male GI between December and January, just as water temperature began to fall from its annual high, suggests a massive spawning, with continued slower release until March, at the latest. A simultaneous decline in large oocytes supports this as the main spawning period. Ripe spermatozoa during winter may have been left after the major spawn. Residual sperm packets in *Anthopleura elegantissima* can be maintained up to four months after spawning, but eventually are resorbed (Jennison, 1979; Sebens, 1981). The actinian *Halcampa duodecimcirrata* contains motile sperm both before and after female spawning (Nyholm, 1949). On the other hand, except for April and May, some males always contained stage 2 and riper sperm. Some sperm of *Urticina crassicornis* are released immature, with excess cytoplasm around the head; their fertilization capability is unknown (Chia and Spaulding, 1972). If further research determined that 1) this occurs in *U. lofotensis,* and 2) the sperm can mature following release, a strategy for fertilization of the eggs that seem to be continually dribbled out would be provided.

High GI did not always coincide with gamete ripeness. The abrupt increase in indices during June may have been due to abundant food. The largest number of *Calliostoma foliatum* shells were recovered from anemones collected then, when three out of six females had loose oocytes in their coelenterons. For males, with only immature sperm follicles, the increase was in gonad quantity but not maturity. Sebens (1981) offered the same explanation for briefly increased volume of immature gonads in *Anthopleura elegantissima.*

Low GI may indicate recent spawning, but handling might induce premature gamete release, and individuals just developing gonads would presumably have a low GI. [Animals lacking gonads were assumed to have either recently spawned (several loose oocytes were found in two of them) or been sexually immature.] Perhaps an anemone attains sexual maturity at a particular size, gradually coming into phase with the rest of the population, as Gonor (1972) found in *Strongylocentrotus purpuratus.* Were this true, small samples containing animals of all sizes would emphasize asynchrony of reproductive cycles. However, gonad indices varied even among anemones of similar sizes collected at the same time. Sterile animals were taken throughout the year.

Speculations on larval development and settlement patterns

Based on published reports and his own findings, Spaulding (1974) ventured that internal brooding is facultative in *Urticina crassicornis.* Stephenson (1928) noted that rather large, unwieldy planulae rich in yolk, such as those of *U. lofotensis* in Europe, are rare except in viviparous forms. Whether he meant to imply that *U. lofotensis* broods is unclear; no reference has been made to this habit by others. There is no evidence that it does so in Carmel Bay.

In the study area, specimens of *Urticina lofotensis* occur more densely in shallow, horizontal depressions of large boulders than on open substrata. Perhaps larvae or adults are carried there by gravity or in eddies. If so, chances of survival should be enhanced because food would be similarly concentrated and the depressions would

provide protection from surge and scour. Alternatively, larval or adult anemones might actively seek depressions [adults can creep on their pedal discs as can many other anemones (Stephenson, 1928; Dunn, 1977)] for the shelter and abundant food they provide.

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